

# THE BEHAVIOR AND ECOLOGY OF HERMIT HUMMINGBIRDS IN THE KANAKU MOUNTAINS, GUYANA.

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FOR nearly three months, 17 January to 5 April 1970, my husband and I camped at the foot of the Kanaku Mountains in southern Guyana. Our camp was situated just inside the forest beside Karusu Creek, a tributary of Moco Moco Creek, at approximately 80 m above sea level. The period of our visit was the end of the main dry season which in this part of Guyana lasts approximately from September or October to April or May.

Although we were both mainly occupied with other observations we hoped to accumulate as much information as possible on the hermit hummingbirds of the area, particularly their feeding niches, nesting and social organization. Previously, while living in Trinidad, we had studied various aspects of the behavior and biology of the three hermit hummingbirds resident there: the breeding season (D. W. Snow and B. K. Snow, 1964), the behavior at singing assemblies of the Little Hermit (*Phaethornis longuemareus*) (D. W. Snow, 1968), the feeding niches (B. K. Snow and D. W. Snow, 1972), the social organization of the Hairy Hermit (*Glaucis hirsuta*) (B. K. Snow, 1973) and its breeding biology (D. W. Snow and B. K. Snow, 1973), and the behavior and breeding of the Guy's Hermit (*Phaethornis guy*) (B. K. Snow, in press).

A total of six hermit hummingbirds were seen in the Karusu Creek study area. Two species, *Phaethornis augusti* and *Phaethornis longuemareus*, were extremely scarce. *P. augusti* was seen feeding once, and what was presumably the same individual was trapped shortly afterwards. In other areas this species is mainly a mountain bird of fairly high levels (600–1500 m) (Meyer de Schauensee, 1948, Phelps and Phelps, 1958, Snyder, 1966), so our record was probably a straggler from higher levels in the Kanakus. *P. longuemareus* was trapped twice but not otherwise seen. In Guyana and Surinam this species is mainly a bird of coastal areas (Snyder, 1966, Haverschmidt, 1968), so the individuals trapped were possibly also vagrants. The four other hermits present, the Hairy Hermit, the Pale-tailed Barbthroat (*Threnetes leucurus*), the Long-tailed Hermit (*Phaethornis superciliosus*), and the Reddish Hermit (*Phaethornis ruber*), were all breeding residents and seen on most days.

Throughout our stay we both made records of all hermit hummingbirds seen feeding and noted the abundance of the different flowers at which they fed. We also hunted for nests and approximately once a week trapped with mist-nets. Leks or singing assemblies of the Reddish and Long-tailed Hermits were found and also the solitary singing perch of a Pale-tailed Barbthroat.

TABLE 1  
WEIGHT, BILL LENGTH, AND NUMBER OF FIELD RECORDS OF HERMIT HUMMINGBIRDS  
RESIDENT IN STUDY AREA

Species	Weight (gm)	Bill length (mm)	Field records		
			Number trapped	Nests	Feeding records
<i>Glaucis hirsuta</i>	6.8 (6.0-8.1)	31	5	3	15
<i>Threnetes leucurus</i>	6.9	27	1	3	8
<i>Phaethornis superciliosus</i>	5.8 (5.2-6.8)	38	16	4	67
<i>Phaethornis ruber</i>	2.7 (2.3-3.1)	23	(2)*	-	29

Weights (range and mean) are of birds trapped during this study; bill-lengths are means of museum specimens.

\* Very small hermits such as *P. ruber* more often bounce out or fly through nets than become entangled in them.

All were visited and watched at fairly regular intervals.

The relative abundance of the four resident species is indicated by the number trapped and the number of feeding records obtained (Table 1). The number of nests found is not a good index of abundance, as the much higher and more exposed nests of the Barbthroat and the Hairy Hermit are undoubtedly easier to find than the lower nests of the Long-tailed and Reddish Hermits.

There have been several publications on the singing assemblies of the Long-tailed Hermit in Guyana. Nicholson (1931) proved by collecting that the large and constant groups of calling birds were in fact assemblies of males. Davis (1934, 1958) published additional information on the calling behavior of the males and the size and abundance of singing assemblies. He also gave an account of the singing assemblies of the Reddish Hermit and described some of the male's displays. His accounts are compared in detail with my observations in the following sections.

The data on feeding niches are presented in relation to more extensive evidence on the feeding niches of the hummingbirds of Trinidad (B. K. Snow and D. W. Snow, 1972). The Trinidad observations showed that the larger hummingbirds feed predominantly on large flowers which are usually red and have a long corolla, and are apparently adapted for pollination by hummingbirds, while the small hummingbirds visit a greater variety of small unspecialized flowers, their shorter beaks apparently excluding them from some of the large flowers.

#### BREEDING SEASON

In Trinidad the breeding season of hummingbirds largely coincides with the main dry season although a substantial number of hermits, particularly

*Glaucis hirsuta*, breed in the first two to three months of the wet season (Snow and Snow, 1964). In Costa Rica the cup-nesting hummingbirds breed almost entirely in the dry season (Skutch, 1950) and the hermits breed in both the dry and wet seasons (Skutch, 1964, 1972), some species i.e. *Threnetes ruckeri* and *Glaucis aenea* exclusively in the latter season. In northern Guyana (Davis, 1934, 1958) the breeding season of hummingbirds largely coincides with the main dry season (August to November) which is shorter here than in the Kanakus. Consistent with this, our observations indicated that January to the beginning of April was the end of the hermit breeding season in the Kanakus. A total of ten occupied hermit nests were found. The calculated months of laying for these nests were: Hairy Hermit, two in February, one in March; Barbthroat, one each in January, February and March; Long-tailed Hermit, two in January and two in February. In early March a Reddish Hermit was seen feeding a juvenile recently out of the nest which gives an approximate laying date in January. Towards the end of March there was a decrease in attendance at the two leks of the Long-tailed and Reddish Hermits and at the solitary singing post of the Barbthroat, which indicates, as do the nesting data, that the breeding season was coming to an end.

A total of 23 hermits were trapped and examined for wing moult. Of these only three Long-tailed Hermits were moulting, one in January and two in March.

#### PALE-TAILED BARBTHROAT (*THRENETES LEUCURUS*)

The Barbthroat found in Guyana, the eastern of the two widespread species of *Threnetes*, has not been studied previously in the field. Those watched in the Kanakus had a considerably brighter throat pattern than specimens from the coastal and lowland areas further north in Guyana, as represented in the British Museum collection; there are no specimens from the Kanakus for comparison. The adult Barbthroats in the Kanakus have a white moustachial streak and a partial white superciliary stripe, a black chin and a blackish area below the conspicuous orange throat band; the four outermost tail feathers appeared to be entirely white except for small dark spots near the tip.

Observations on the western species, *Threnetes ruckeri*, in Costa Rica (Skutch, 1964) showed that first one and in subsequent years two then three males called in the same patch of forest, but not close together, over 15 years. My observations in Guyana suggested that *T. leucurus* has a similar kind of behavior. One adult male Barbthroat was discovered singing on 3 February in mature forest about half a mile from Karusu Creek. The canopy was unbroken in the area, so the undergrowth was thin. The bird sang within an area approximately  $9 \times 2$  m where he had three commonly used perches, slender horizontal twigs 60 to 80 cm above the ground.

Throughout February and March weekly watches of at least an hour, covering both the morning and afternoon, were made at this singing territory. Up until the last week of March the adult was present at all watches. The average attendance was 73 percent of afternoon and 62 percent of morning watches. This difference was due to the persistent visits of a young male in the mornings, for the adult was frequently absent chasing this bird. During the last week of March the young male took over the singing territory.

*Young males.*—In plumage the young male differed from the adult male in having a much larger area of the outer tail feathers dark instead of white, and in having a more extensive area of white behind and below the eye. That these were immature characteristics was confirmed at a nest of the species where one of the young after leaving the nest stayed in the vicinity for a week and allowed close examination. Besides the above characteristics this juvenile had a warm buff instead of orange throat band.

*Song.*—The adult male's song was a brief rather high-pitched phrase repeated many times. This phrase, sounding something like *zit-zit-zeri*, lasted approximately  $1\frac{1}{2}$  seconds and was repeated anything from once or twice a minute up to a maximum of 33 phrases a minute. The singing rate was generally higher in the morning, around 15 phrases per minute, compared to the afternoon when it dropped to one or two per minute. If any species of hummingbird came into the vicinity the male immediately increased his singing rate to a maximum. The song of the young male was a hesitant quieter version of the adult song. About two miles further up Karusu Creek another adult male Barbthroat was discovered singing in a flat area of forest near the river. Its song phrase, which sounded like *zer-zee-zer-zeri*, was noticeably different from that of the first adult, except for the terminal *zeri*. The song of *Threnetes ruckeri* in Costa Rica is apparently very different. Skutch (1964) describes it as a sweet warbler-like song, each phrase lasting four or five seconds and always spaced by intervals of silence longer than the song.

Like all other hermits that I have so far encountered, the Pale-tailed Barbthroat has a flight call, a single *seep* or *weep*, which is uttered by male or female when flying about in the forest.

*Display.*—While singing the male wags his tail up and down. At the approach of any other hummingbird there is an increase of tail movement and it is also spread so that the white outer tail feathers are displayed.

Throughout the period of observations on the adult male an immature male was frequently in the vicinity of the singing territory, usually coming and singing in it when the adult was absent. During the final period of observation when the immature had taken over the singing territory, he was visited by a juvenile Barbthroat with a pale buff instead of orange throat band.

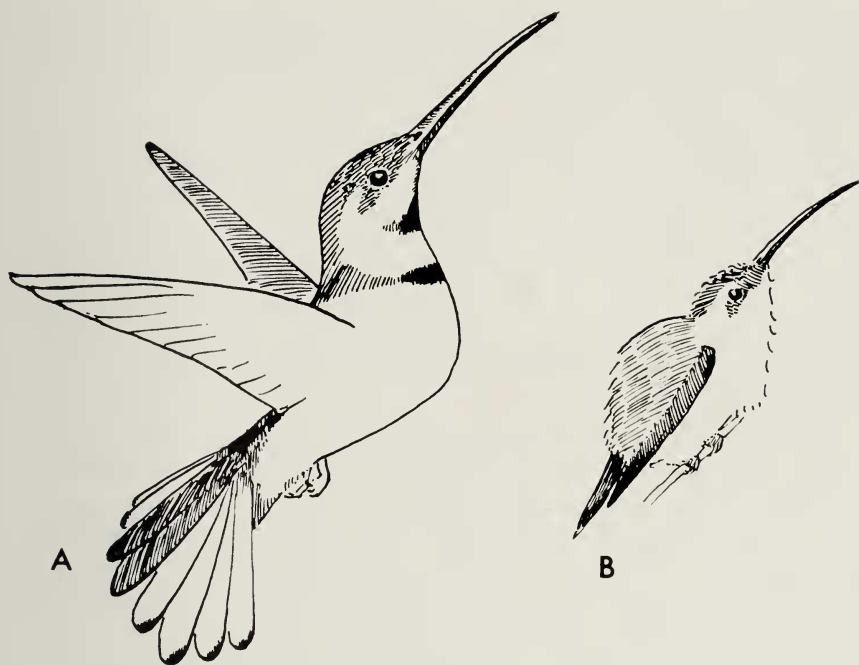


FIG. 1. a. A hovering male Pale-tailed Barbthroat displaying the throat pattern. b. The posture of a male Reddish Hermit singing at the lek.

All display and social interactions observed appeared to be between these birds and no known female visited the singing territory although the juvenile could have been a female.

When another Barbthroat visits a singing male, the latter hovers off his perch with tail fanned, draws his head sharply backwards and at the same time throws his breast forward, so displaying the striking throat pattern (Fig. 1 a). This is accompanied by a very quiet version of the normal song phrase. Meantime the visitor hovers in front of the owning male who always maintains a position below the visitor. Usually the visitor then flies away, chased by the owning male still with tail spread and uttering the muted song. The encounter between the juvenile-plumaged bird and the young male culminated in a brief mounting. The juvenile flew into the singing territory and perched there silently for a minute with its tail wagging up and down. It then flew over to the young male who was singing and briefly hovered down on to his back; the young male hovered up and his place on the perch was taken by the juvenile. The young male then hovered with tail fanned facing the juvenile and displaying the throat pattern, meantime

uttering the muted song. He then hovered, still singing, round and onto the juvenile's back, hovering there briefly before the juvenile flew off followed by the young male. This sequence, or something closely akin to it, is probably the pre-copulatory display.

Twice the adult male was seen to behave as though mating with a leaf, each time with the same dead leaf caught over a twig. Before each leaf-mating he hovered with tail fanned, uttering the muted song over the dead leaf, and briefly hovered down onto it. These leaf-matings occurred once in the middle and once after a period of normal advertising song. Male Guy's Hermits also quite frequently behave as though mating with leaves. These leaf-matings occur within a male's singing territory and the same leaf is used repeatedly. The behavior that immediately precedes leaf-mating is similar to the pre-mating display.

In the four *Phaethornis* species so far studied, *P. guy*, *P. superciliosus*, *P. ruber*, and *P. longuemareus*, all of which have colorful gapes and congregate at singing assemblies, the males all display their gapes, by opening their beaks wide, to other individuals who visit them at their singing perches. The Barbthroat, with a pale drab-colored gape, does not display it; instead the beak is kept closed and the throat pattern is displayed. It is the only species of hermit with a colorful and contrasting throat pattern, which seems to be functionally analogous to the colored gape of the other species, so some behavior that displays it is to be expected. The Hairy Hermit (*Glaucis hirsuta*) which is almost certainly closely related to the Barbtthroats, does not display its gape either.

#### LONG-TAILED HERMIT (*PHAETHORNIS SUPERCILIOSUS*)

The singing assembly or lek of the Long-tailed Hermits was a large one stretching along one bank of Karusu Creek for at least a 100 m. It was in primary forest mostly on a steep slope coming down to the river. It was two miles up the valley from our camp where two nests were found and many of the feeding records were obtained, yet it appeared to serve this area as the local Amerindian who lived with us in camp did not know of another singing assembly in the valley.

The males called at perches about 9 to 10 m apart and most were in view of their neighbors. They called from slender twigs with an uncluttered horizontal section of about 45 cm, a feature that is possibly of importance during the visiting behavior described below.

Calling and attendance at the singing assembly was high from mid-January to mid-March but dropped sharply towards the end of March. The call was a rapidly repeated *chip chip chip* or *chit chit chit* etc. This suggests a different note from the *jang jang* etc as interpreted by Nicholson (1931) at the singing

assemblies in northern Guyana. Each *chip* lasts about one-fourth to one-third of a second and between 92 and 102 were uttered per minute. It was noted that a bird often adjusted his calls with his closest neighbor so that the calls alternated and did not overlap. Another sweeter and quieter call *who-ee who-ee* etc was heard at the singing assembly. This is undoubtedly the *who-dee* described by Nicholson (1931). The *who-ee* was always uttered in flight, either during chases or when the male was flying for any other reason within the precincts of the singing assembly but not outside it. Another flight call, *switch*, is uttered by both males and females when flying through any other part of the forest but the singing assembly.

While at their singing perches the males call very persistently, continuing to call during such activities as stretching, preening, head scratching, and wiping the beak. A watch on one male from 09:00 to 10:00 in February showed that it was present and singing for 73 percent of the hour with five absences averaging three minutes each. During a watch at the same time on 17 March a nearby male was present only 41 percent of the hour and the male watched previously was present only 30 percent of half an hour.

*Display*.—A number of males were seen to visit each other at their lek perches. Once a bird that had not been singing at a neighboring perch, so might have been a female, was seen to visit. In all cases, the visitor flew up and landed on the same twig about 5 cm from a calling male. As the visitor approached, the calling male spread his tail and rapidly fanned it up and down, then as the visitor landed the owning male opened his beak and displayed his orange-red gape. The visitor then touched the inside of the displayed gape either with its tongue or the tip of its beak. Once the visitor also displayed its gape. Visits ended by the visitor flying away, the owner usually staying but sometimes following.

#### REDDISH HERMIT (*PHAETHORNIS RUBER*)

The singing assembly of the Reddish Hermit was in dry scrubby forest, probably secondary, about half a mile from Karusu Creek. Five visits were made to this assembly between 13 February and the end of March. There were four adult males and one probable young male present on the first three visits, three adults and a young male on the fourth visit, and only the young male on the final visit on 26 March. The general level of singing decreased during the period and displays at the assembly were only seen on the first three visits.

The assembly covered an area of approximately 30 m by 45 m. Individual calling territories were approximately 15 by 15 m. The assembly was in an area of dense low undergrowth and usually individuals were audible but not visible to their neighbors. Individual birds appeared to occupy the same

territories at each visit; in the case of the young bird with a slightly different song this could be verified.

The song, interpreted as *zee zee zee zeezeze*, consists of three notes coming down in scale, each lasting about half a second, followed by a fourth shorter note which is joined to a jumble of still shorter notes also coming down in scale. The whole phrase lasts  $2\frac{1}{2}$  to  $2\frac{3}{4}$  seconds and a usual rate of calling was eight or nine phrases in 30 seconds. The phrase of the bird believed to be a young male lasted  $4\frac{1}{2}$  seconds. It was believed to be a young male because of its slower call and its occupation of the singing assembly after the adult males had deserted it, as both are characteristics of young male *Phaethornis guy* (B. K. Snow, in press). When two neighbors audible to each other are singing at the same time they often sing their phrases alternately so that they do not overlap. The Reddish Hermit's song at this assembly appears to be very similar to its song near Bartica in northern Guyana, described by Nicholson (1931) as *see-see-see-seezere*. However it is different from the song of a captive bird from Brazil which is described by Mobbs (1971) as *sweep, sweep, sweep, swee-e-ep, see-e-e-e-p, swee-e-e-e-p*.

The very characteristic posture adopted for singing is shown in Figure 1 b. While singing the bird looks intently upwards, turning his head slightly from side to side. A male does not have a favorite or usual perch for singing but uses a number of perches within his territory, and he frequently flies, usually still singing, from one perch to another. When a male first returns to his singing perch the white thigh feathers are not visible but as he starts singing he displays them conspicuously. When a male on his singing perch scratched his head with his foot, he retracted the white thigh feathers on the scratching leg so they were no longer visible but when the foot was restored to the perch he extended them again.

No perched display was seen and Mobbs (1971) has not seen his captive birds do a perched display. Davis's description (1934) of a perched display is extremely like the stretching movement of hermit hummingbirds. This movement, which consists of arching both wings over the back while the head is thrust out and the tail fanned and depressed, often culminates in a general shaking or vibrating of all the feathers. I have seen similar stretching movements done by four species of *Phaethornis* where the males sing at leks, *P. guy*, *P. superciliosus*, *P. ruber*, and *P. longuemareus*, and in all it is diagnostic of imminent flight. The Barbthroat stretches in the same way before flying off from his solitary singing post. Twice male Reddish Hermits did another stretching movement before leaving. They pointed their beaks upwards and distended outwards the flexible rami of the lower mandible while the rest of the beak remained closed. Skutch (1964) has described a similar yawning movement in *Threnetes ruckeri*.



*Aerial displays.*—The Reddish Hermit's aerial displays are extremely elaborate. A detailed description of aerial displays culminating in a false mating performed by a captive male from Brazil has been given by Mobbs (1971). Davis (1958) has also described aerial displays which took place in front of a female but nowhere near any known singing assembly. From this he concluded that aerial courtship displays were always performed only to females at some place remote from a singing assembly. My observations, described below, show this not to be so. Two variations of an aerial display were seen; each was seen twice and occurred at or near a singing perch. One was accompanied by a musical warbling, a soft just audible *weep weep* etc, each call well spaced from the next. This was a much sweeter call than the song, strongly reminiscent of the alarm call of the Willow Warbler or Chiffchaff (*Phylloscopus* spp.).

The display was performed by a visiting bird, apparently a neighboring male, in front of the owning male on his perch. The visitor hovered with his tail spread and cocked over his back and his yellow gape displayed upwards, 8–10 cm above and in front of the owning male. In displaying the gape the rami of the lower mandible were spread wide apart so they were about four times further apart than when the beak is closed. While it hovered the bird's rear swayed from side to side by about an inch while the head remained stationary. The sweet *weep* appeared to be uttered by the perched bird in time with the swaying of the hovering bird.

This display is close to performance (a) described by Mobbs except that his male made a twittering noise that accompanied the movement. Davis describes a similar display by a male in front of a probable female; he also thought the perched bird was uttering the subdued warbling that accompanied the performance, so possibly the call can be made by either bird.

In the other aerial display, which was silent, both birds involved hovered facing each other between 25 to 150 mm apart. The lower bird displayed its gape and had its tail raised and fanned, so was fundamentally in the same position as the airborne bird described above; the upper bird intermittently protruded its white tongue. One incident took place after three birds had been chasing each other and the participants were not identified. The other incident occurred between a male that had been watched for the previous 40 minutes in his singing territory, where the incident took place, and another bird probably a neighbor.

Both Mobbs and Davis describe the protrusion of the tongue during aerial displays. The Long-tailed Hermit also protrudes its tongue during the visiting display. In the Guy's Hermit (B. K. Snow, in press) the males visit each other at their singing perches and perform the same display sequence as at the visit of a female which may culminate in mating, and probably some or all

TABLE 2  
FLOWER CHARACTERISTICS AND FEEDING RECORDS OF THREE HERMIT HUMMINGBIRDS

	Color	Corolla		Timed feeds (seconds)	<i>Glaucis hirsuta</i>	<i>Phae- thornis super- ciliosus</i>	<i>Phae- thornis ruber</i>
		lgth	width				
Acanthaceae							
<i>Trichanthera gigantea</i>	pink	15	3	½-1	1	13	15
Red vine	red	60	3		1	2	
Passifloraceae							
<i>Passiflora longiracemosa</i>	red	44	11	5-12	4	29	
Verbenaceae							
<i>Petreaa macrostachya</i>	purple					1	2
Musaceae							
<i>Heliconia bihai</i>	red	40	5	4-5		2	
<i>Heliconia</i> sp.	blue	39	5	3-6	1	1	
Zingiberaceae							
<i>Costus spiralis</i>	red	35	5	1-1½	6	15	2
Unidentified						1	6
Insect searching records					2	3	3
Total nectar feeding records					13	64	26
Number of plant species					5	9	9

of these displays of the Reddish Hermit are performed to females prior to mating. Mobbs' captive bird frequently followed aerial display by a stylized mating movement on the perch.

It was found in the Guy's Hermit that during the period when young males begin to attend the singing assemblies and call there they also occasionally call and display elsewhere. This period coincides with the end of the breeding season. The aerial display of the Reddish Hermit away from the singing assemblies described by Davis occurred in September and October, which from the nests he records is also the end of the breeding season in that part of Guyana; so it may have been the display of young birds.

#### AVAILABLE FLOWERS AND THEIR NECTAR POTENTIAL

The nectar potential of a flower was assessed by measuring the length of its corolla tube and its width near the base and also by timing the length of a hummingbird's feed at it, from insertion to withdrawal of the beak. This information was obtained for most of the flowers where there were three or more feeding records (Table 2).

The most abundant riverside plant in the forest was *Costus spiralis*. It

was flowering throughout our stay. An idea of its abundance is indicated by a count on 17 March of 114 plants with flowering heads along approximately a mile of Karusu creek immediately downstream from the Long-tailed Hermit's singing grounds. This plant was also very abundant along the gullies that ran into the main stream. A timed feed of a Hairy Hermit at *Costus* was 1–1½ seconds.

Where the river received ample sunshine, usually due to felling, the shrub *Trichanthera gigantea* was abundant. It was flowering when we arrived in January but most flowers were over by mid-March. Individual flowers opened in the afternoon around 3 o'clock and were over and dropped soon after 8 o'clock the following morning. The flower has two nectaries (3 mm across) at the base of two groups of stamens. Evidence of timed feeds, ½–1 second for the Reddish and Long-tailed Hermits, suggests that only a small amount of nectar is available. This is probably the reason for the lack of feeding records for the two larger hermits.

*Passiflora longiracemosa* is a liana that climbs to canopy level but produces its flowers at ground level. It was found flowering soon after we arrived and it continued to flower until the end of March. It was common in luxuriant primary forest and was also found in some dryer forest fringing the savannah which may have been secondary. It was apparently a rich source of nectar; the average of 12 timed feeds of the Long-tailed Hermit was 7 seconds. Birds were re-visiting the same flower at approximately half-hour intervals.

An unidentified *Heliconia* species which had hanging purplish blue flowers did not grow on the banks of the river but set back from it 10 meters or more; it also grew along the gullies that opened into the river. It was not particularly abundant. It started to flower at the beginning of February and continued to do so until we left. The timed feeds at this flower of the three big hermits were 3, 4, and 6 seconds. A few clumps of *Heliconia bihai* were found, mostly up side gullies. This plant is very abundant in Trinidad, where our records showed it to be the most important nectar source for the two large resident hermits, *G. hirsuta* and *P. guy*. Timed feeds at this plant from both Guyana and Trinidad averaged 5 seconds.

A red-flowered vine (Acanthaceae) bloomed from the first week of February until the end of March and was quite common in the forest. The long corolla tube had a 15 mm curvature and the flower looked as if it was adapted to pollination by long-billed hermits, but not many were seen feeding at it.

The flowers described above were fairly certainly the major source of nectar for hermits in the study area during February and March. Both of us spent all the hours of daylight in the forest or its edges and normally interrupted other observation to note the activity of any hermit hummingbird

that came into view. As all the hermits make a flight call when flying about feeding they are not readily overlooked.

#### FEEDING NICHES

Table 2 gives the number of feeding records obtained at the different flowers. Only eight feeding records were obtained for the Barbthroat so they have not been included. Two of the eight were nectar-feeding records, one at the unidentified *Heliconia*, and one at *Costus spiralis*. Once the Barbthroat was seen sucking sap at a recently broken branch and the remainder of the records were of insect searching. The preponderance of insect searching records is interesting in view of the Barbthroat's relative scarcity. In a study of the feeding niches of tanagers and honeycreepers in Trinidad (B. K. Snow and D. W. Snow, 1971) it was found that the species taking the largest proportion of insect food were the least abundant; conversely species mostly feeding on nectar or fruit were the most abundant. Skutch's observations in Costa Rica and Panama also suggest that *Threnetes ruckeri* feeds more on insects than nectar.

Besides the flowers shown in Table 2 the Reddish Hermit was seen feeding once or twice at six other species; three different species of Marantaceae with yellow or white flowers, a white-flowered papilionate vine, the greenish yellow flowers of the papaw (*Carica papaya*), and the yellow flowered vine *Mandevilla scabra*, which it exploited by piercing the base of the corolla tube. Of the flowers it fed on only *Costus spiralis* has a red inflorescence with long corolla tube and is probably adapted to pollination by hummingbirds. With a bill length of 23 mm the Reddish Hermit is most likely excluded from *Passiflora longiracemosa*, whose corolla tube is very long, and possibly from the Heliconias. It was once seen probing, apparently unsuccessfully, at the base of the long corolla of the red-flowered acanthaceous vine. The very small hermit *Phaethornis longuemareus*, studied in Trinidad, also differed from the two larger hermits (*G. hirsuta* and *P. guy*) in taking nectar from a larger variety of flowers, and a larger proportion of them were small flowered without red inflorescences. The evidence on the feeding niche of the Reddish Hermit in the Kanakus suggests that the same sort of differences separate its feeding niche from that of the Hairy and Long-tailed Hermits.

In a study of the feeding niche of the Hairy Hermit in Trinidad 50 percent of the 236 nectar records were from *Heliconia bihai*. This plant was scarce in the Kanaku study area compared to Trinidad, which may partly account for the Hairy Hermit's relatively low numbers. The two most abundant nectar source plants in the area, *Costus* and *Trichanthera*, were assessed as having a relatively low nectar potential, particularly the latter, so possibly in terms of

energy expenditure were uneconomic for the heavy Hairy Hermit to exploit. *Costus spiralis* also grew in Trinidad but only 7 percent of the Hairy Hermit nectar feeding records were from it.

The lighter weight and longer bill of the Long-tailed Hermit compared to the two other larger hermits of the area (Table 1) are probably advantageous to it in exploiting the available nectar of the area. Its longer bill probably means a more efficient feeding at the flowers with very long corollas, i.e. *Passiflora*, *Heliconia*, and the acanthaceous vine, and its lighter weight would entail less energy outlay for hovering at such flowers as *Trichanthera gigantea* where there was evidently only a small quantity of honey to be obtained per probe.

#### ABUNDANCE IN RELATION TO SOCIAL BEHAVIOR

Population density probably has an important influence on the development of lek behavior in hermit hummingbirds. Thus the most abundant hermit in our study area, the Long-tailed, had the biggest lek with the shortest distance between singing males. The next most abundant species, the Reddish Hermit, had a smaller lek with larger individual singing territories within the lek. The relative abundance of these two hermits in the area studied is probably representative of much of Guyana, as Davis (1934, 1958) during his long experience of the forest found 32 leks of the Long-tailed Hermits, many of them large and possibly exceeding 100 birds, and only two leks of the Reddish Hermit, one large, of approximately 60 birds, and one of about a dozen birds.

Neither of the two less abundant hermits of the area, the Hairy Hermit and the Barbthroat, has communal leks. The Barbthroat's relative scarcity probably accounts for its advertising at solitary singing perches, which Skutch's data suggest are traditional and can fulfil the same function as a lek as a meeting place for the sexes. The lack of lek advertising in the Hairy Hermit is because the males hold a section of suitable riverside territory where one or more females nest, the male closely defending these nests (B. K. Snow, 1972). This situation, first studied in Trinidad, also applied to the Kanakus although the species was far less abundant here.

The nests of the Hairy Hermit and the Barbthroat are almost identical, but there is a difference in the siting of the nests which may have influenced their social behavior. The four nests of the Hairy Hermit found in the area were overhanging the river. The same preference was found in Trinidad where 345 nests were all either over or very close to forest streams or to roads through the forest, which are steep banked and have many features similar to a stream (D. W. Snow and B. K. Snow, 1973). On the other hand, none

of the three nests of the Barbthroat found in the forest was beside a stream; all were on the fronds of small understory palms which were scattered regularly throughout the forest area studied. Competition between Hairy Hermits for the relatively scarce riverside nest-sites must be quite high and has probably led to the male's participation in nest defense. On the other hand there can be no scarcity, therefore little competition, for the Barbthroat nest-sites, so the male would have no useful role at the nest.

#### SUMMARY

During a three-month visit to the Kanaku Mountains in southern Guyana (January–April 1970) observations were made on the four species of hermit hummingbirds resident in forest at the foot of the mountains: *Glaucis hirsuta*, *Threnetes leucurus*, *Phaethornis superciliosus*, and *P. ruber*. Two other species, *P. augusti* and *P. longuemareus*, were recorded but were scarce and probably not resident. The period of observation coincided with the end of the breeding season.

Observations were made at the solitary song-perch of a *Threnetes leucurus*, which was occupied first by an adult and then by an immature bird and was visited by a third, juvenile bird. In display this species exhibits the contrasting throat-pattern, which seems to serve the same function as the colorful gape exhibited in display by *Phaethornis* species. Its general behavior is similar to that of *T. ruckeri* in Central America.

Regular observations were made at a very large singing assembly of *P. superciliosus*, and a very small assembly of *P. ruber* (five birds). The songs and behavior of these species are compared with previously published accounts.

The relative abundance of the four hermit species was assessed from the size of the singing assemblies, the number of feeding records, and the number of birds trapped. *T. leucurus*, the least abundant of the four, is probably mainly insectivorous. It is suggested that the development of lek behavior (or its absence) is related to the population density of the different species.

Of the two species which do not show lek behavior, *G. hirsuta* has linear nesting territories along streams, while the nests of *T. leucurus* are dispersed throughout the forest. It is suggested that the male's active role at the nest in *G. hirsuta*, in contrast to *T. leucurus*, is related to the relative scarcity and the need for defense of stream-side nest-sites.

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### CORRIGENDUM

The scientific name of the Adelle Penguin, *Wilson Bull.* 94:309, 1972 should be *Pygoscelis adeliae*.

### PUBLICATION NOTES AND NOTICES

A BIBLIOGRAPHY OF ARIZONA ORNITHOLOGY. ANNOTATED. By Anders H. Anderson. The University of Arizona Press, Tucson, Ariz., 1972: 6 × 9 in., x + 241 pp. Paper cover. \$7.95.

This book lists an estimated 2,500 references to Arizona ornithology, grouped in ten sections according to subject. Even papers that are marginally about Arizona birds are included, such as morphological studies in which the specimens came from that State. The author has set forth in the Preface his decisions on what to include and what not to include. His annotations are concise and useful. The lack of cross references is a minor inconvenience.—P.S.